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COEXISTENCE OF THREE PREDATORS COMPETING FOR A SINGLE BIOTIC RESOURCE

CLAUDE LOBRY, TEWFIK SARI, AND KARIM YADI

Abstract. We construct a model of competition of three consumers for one single biotic resource ; simulations show that the three species coexist. Using singular perturbations theory we sketch a mathematical proof for this coexistence. The main mathematical tool used is an extension of the Pontryagin-Rodygin theorem on the "slow" motion of a "slow-fast" differential system when the "fast" motion possesses a stable limit cycle. The mathematical analysis is done within the framework of Non Standard Analysis.

1. Introduction

The question of coexistence of competing species for a single resource has a very long history that we shall not attempt to recall here. We just recall the two decisive papers by Armstrong and Mac Gehee [1, 6] where they pointed that *coexistence is not synonymous of coexistence at equilibrium.* These papers were the starting point of numerous papers showing complex behaviors of systems of competitors and evidence of coexistence on the basis of numerical simulations. Following this tradition we propose a model of coexistence of three species competing for one resource.

The present paper has two parts. In the first part we construct our model and explain what is the rationale behind our construction ; each step is illustrated by simulations. In the second part we consider our model as a member of a more general "consumer-resource" model for which we explain how coexistence of species can be proved using singular perturbation analysis ; as an essential tool we use an extension of a theorem of Pontryagin and Rodygin.

Considered from the ecological point of view our model shows that oscillations in a "consumer-resource" relationship can open the door to coexistence with other species provided that the new introduced species do not perturb too much the oscillations. We do not know any example of an interaction between four species of the type of the model presented here but its existence is plausible. We shall explain it during the construction of a model. But we must acknowledge here that what we do is a kind of "virtual ecology" showing what is "theoretically possible" in a world of species respecting basic facts well established in concrete ecology. *It is not a description of the real world !*

From the mathematical point of view our paper can be considered as an application of singular perturbation methods to the mathematical proof of persistence for some specific system. Our contribution consists mainly in the analysis of the

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theorem of Pontryagin and Rodygin and its extension to a theorem which is more effective in some circumstances. Detailed proofs can be consulted at [14] and will be published elsewhere. The mathematical analysis is done within the framework of Non Standard Analysis, using the axiomatic of Nelson [7] and respecting the spirit of G. Reeb [9].

2. Construction of a model.

2.1. The basic oscillating pair.

We consider the system :

$$\left\{\begin{array}{rcl}\dfrac{ds}{dt} & = & 3s(1-s) - \frac{s^2}{0.01+s^2}x_1 \\ \dfrac{dx_1}{dt} & = & 0.1[\frac{s^2}{0.01+s^2} - 0.65]x_1\end{array}\right. \qquad (1)$$

Due to the presence of the factor 0.1, it can be considered as a "slow-fast" system of two differential equations of the following type :

$$\left\{\begin{array}{rcl}\dfrac{ds}{dt} & = & \frac{1}{\varepsilon_1}[f(s) - g_1(s)x_1] \\ \dfrac{dx_1}{dt} & = & (g_1(s) - d_1)x_1\end{array}\right.$$

where ε_1 is a "small" parameter. The real s represents the density of some biotic resource (prey) for a consumer which density is represented by x_1. This is a rather classical prey-predator model and it is well known that this kind of generalization of the Lotka-Volterra model can have sustained oscillations. The existence of oscillations in prey-predator interaction is clearly demonstrated in laboratory experiments (see [4]), if not in the real world. The choice of the function :

$$g_1(s) = \frac{s^2}{0.01+s^2}$$

in place of the more classical Monod's function with s in place of s^2 was made in order that the nullcline $[f(s) - g_1(s)x_1] = 0$ has the "S-shape" shown on Fig. 1 which prevents the resource from extinction. This kind of assumption is sometimes called the "Allee" effect in ecological literature.

2.2. Addition of a new consumer "x_2".

We want to add a new consumer and at the same time keep the oscillations of (s, x_1). It can be done by introducing a new species with a *very slow* dynamics compare to that of (s, x_1) like in the model :

$$\left\{\begin{array}{rcl}\dfrac{ds}{dt} & = & \frac{1}{\varepsilon_1}[f(s) - g_1(s)x_1 - g_2(s)x_2] \\ \dfrac{dx_1}{dt} & = & (g_1(s) - d_1)x_1 \\ \dfrac{dx_2}{dt} & = & \varepsilon_2\,(g_2(s) - d_2)x_2\end{array}\right.$$

where ε_2 is small.

The existence of two consumers (which densities are represented by x_1 and x_2) of the same resource and having very different characteristic time seems to be common in nature. For instance small mammals and big mammals eating the same grass have a lifespan which may differ of an order of magnitude.

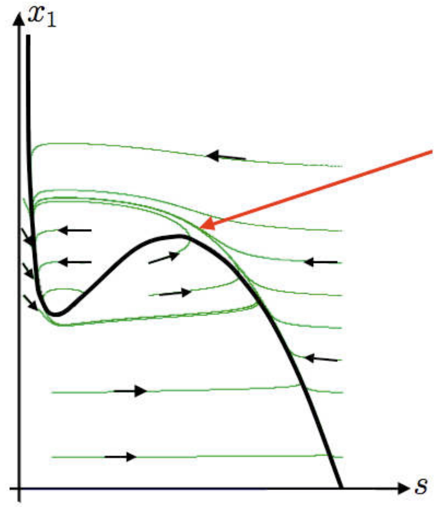

FIGURE 1. On this picture one observes a simulation of few trajectories of the system (1). The black "S-shaped" curve is the nullcline $[f(s) - g_1(s)x_1] = 0$. The direction of the motion along trajectories is indicated by the black arrows and the limit cycle by the red arrow. By the way $s(t)$ oscillates between two values.

Denote by $\overline{x}_2$ some constant x_2 ; since $x_2(t)$ is quasi constant, for a while, the evolution of (s, x_1) is governed by :

$$\left\{\begin{array}{lcl} \dfrac{ds}{dt} & = & \frac{1}{\varepsilon_1}[f(s) - g_1(s)x_1 - g_2(s)\overline{x}_2] \\ \dfrac{dx_1}{dt} & = & (g_1(s) - d_1)x_1 \end{array}\right.$$

In that system we see that when $\overline{x}_2$ is small the nullcline

$$f(s) - g_1(s)x_1 - g_2(s)\overline{x}_2 = 0 \tag{2}$$

is very close to the nullcline

$$f(s) - g_1(s)x_1 = 0 \tag{3}$$

and, thus, oscillations are preserved. The range of oscillations of s is slightly shortened as $\overline{x}_2$ increases. Now, if we look at the process from the point of view of x_2 during an oscillation of period T the growth is given by :

$$\int_t^{t+T} (g_2(s(\tau)) - d_2)x_2(\tau)d\tau$$

which varies monotonically according to the variation of amplitude of s. Thus the growth can be positive for small values of x_2 and negative for large ones ; in the

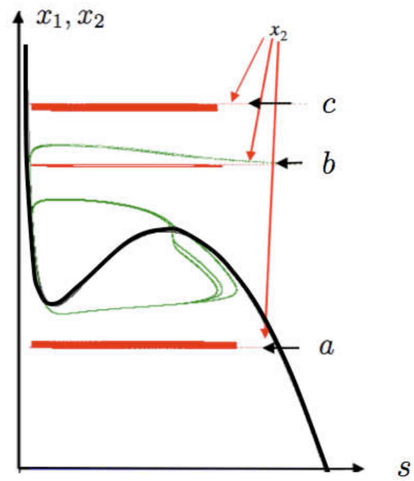

FIGURE 2. Simulation of the system (4). The picture shows the two projections of the trajectories, in green on the plane (s, x_1) and in red on the plane (s, x_2). While the initial conditions where kept constant for s and x_1 they where changed for x_2. One sees that, starting from a small $x_2 = a$ then $x_2(t)$ is increasing and, conversely, starting from a big $x_2 = c$ then $x_2(t)$ is decreasing.

middle there must be an equilibrium. This is the case for the model :

$$(4) \qquad \begin{cases} \dfrac{ds}{dt} &= 3s(1-s) - \frac{s^2}{0.01+s^2}x_1 - g_2(s)x_2 \\ \dfrac{dx_1}{dt} &= 0.1[\frac{s^2}{0.01+s^2} - 0.65]x_1 \\ \dfrac{dx_2}{dt} &= 0.01[g_2(s) - 0.025]x_2 \end{cases}$$

with

$$\begin{cases} s < 0.5 \quad \Rightarrow \quad g_2(s) = 0 \\ s \geq 0.5 \quad \Rightarrow \quad g_2(s) = \frac{0.1(s-0.5)}{0.01+(s-0.5)} \end{cases}$$

We choose $g_2 = 0$ on $[0, 0.5]$ in order to be sure that the nullcline (2) is exactly the same than the nullcline (3) and remains "S-shaped" ; thus oscillations are preserved. This artificial choice is convenient for simplicity but a model with g_2 being smoother would also work. Evidence of coexistence of x_1 and x_2 is given on Fig. 2. On this simulation three initial conditions where taken, keeping $s(0)$ and $x_1(0)$ constant and changing $x_2(0)$. On the picture we have superimposed the projections on the (s, x_1) plane (in green) and the (s, x_2) plane in red. The first initial condition for x_3 is a which is shown by the black arrow ; since the variation of x_2 is very slow the red projection looks like a point moving right to left and left to right very fast while moving up very slowly ; the thick red line corresponds to a dozen of oscillations. Starting from c we see that the point is slowly moving down. Starting from b we see that x_2 remains constant.

2.3. **Addition of a new consumer "x_3".** The idea is to have a new consumer with a g_3 growth rate such that the two graphs of g_2 and g_3 cross like on Fig. 3

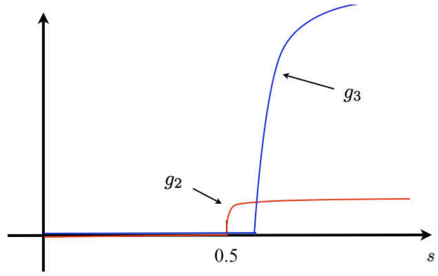

FIGURE 3. The graphs of g_2 and g_3.

in order that during an oscillation of (s, x_1) the species 2 and 3 take the advantage alternatively. This leads to the system :

$$(5)\qquad \begin{cases} \dfrac{ds}{dt} &= 3s(1-s) - \frac{s^2}{0.01+s^2}x_1 - g_3(s)x_3 \\ \dfrac{dx_1}{dt} &= 0.1[\frac{s^2}{0.01+s^2} - 0.65]x_1 \\ \dfrac{dx_3}{dt} &= 0.01[g_3(s) - 0.025]x_3 \end{cases}$$

with

$$\begin{cases} s < 0.58 & \Rightarrow \quad g_3(s) = 0 \\ s \geq 0.58 & \Rightarrow \quad g_3(s) = \frac{2(s-0.58)}{0.01+(s-0.58)} \end{cases}$$

On Fig.4 one sees that the behavior of the system (s, x_1, x_3) is similar to the behavior we observed for (s, x_1, x_2) ; the projection (in blue) on the (s, x_3) plane is similar to the projection (in red) observed for (s, x_2) in Fig.2.

2.4. **Coexistence of all the three consumers.** Now we consider the complete system :

$$(6)\qquad \begin{cases} \frac{ds}{dt} &= 3s(1-s) - \frac{s^2}{0.01+s^2}x_1 - g_2(s)x_2 - g_3(s)x_3 \\ \frac{dx_1}{dt} &= 0.1[\frac{s^2}{0.01+s^2} - 0.65]x_1 \\ \frac{dx_2}{dt} &= 0.01[g_2(s) - 0.025]x_2 \\ \frac{dx_3}{dt} &= 0.01[g_3(s) - 0.025]x_3 \end{cases}$$

Species x_2 and x_3 have a "slow motion" which can be approximated by computing suitable integrals along the basic cycle ; this determines a flow on (x_2, x_3) plane ; this flow is studied and proved to have a stable equilibrium which proves the persistence of both x_2 and x_3. On Fig.5 one sees the projection on the (x_2, x_3) plane of the full system (6) with the three competitors. The simulations from various initial conditions shows convergence to a point which actually corresponds to a periodic orbit in the full space (s, x_1, x_2, x_3). More details are given in the next section.

2.5. **Species 2 and 3 alone.** Consider the system with s, x_2 and x_3 alone in the absence of the species represented by x_1. One easily check that in this case, from the choice of g_2 and g_3, there is no oscillation and the stable equilibrium is the one for which species x_2 wins the competition.

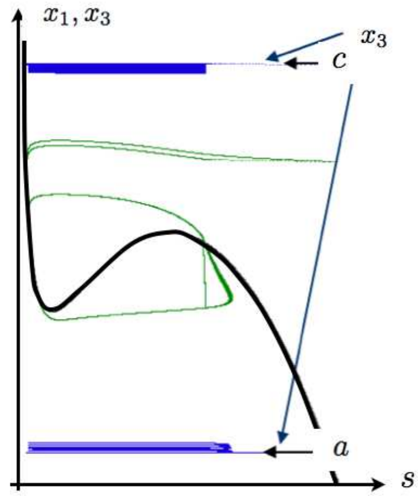

Figure 4. Simulation of the system (5). The picture shows the two projections of the trajectories, in green on the plane (s, x_1) and in blue on the plane (s, x_3). The projection (in blue) on the (s, x_3) plane is similar to the projection (in red) observed for (s, x_2) in Fig.2. Starting from a small $x_3 = a$ then $x_3(t)$ is increasing and, conversely, starting from a big $x_3 = c$ then $x_3(t)$ is decreasing. Between a and c there is some initial condition (not represented) for which x_3 do not increase nor decrease.

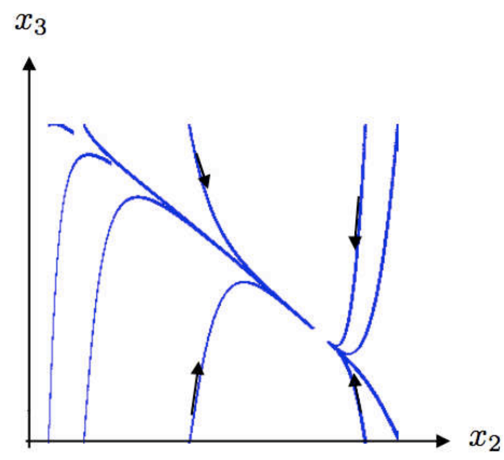

Figure 5. On this picture we have represented the projection of simulations of the the complete system (6) on the plane (x_2, x_3). The variables (s_1, x_1) (not represented) present rapid oscillations while (x_2, x_3) evolves slowly. One sees that all the trajectories seem to converge to an equilibrium. Compare to the "theoretical" picture on Fig 8.

3. PROOF OF THE PERSISTENCE OF THE THREE COMPETITORS IN A MODEL WITH THREE TIME SCALES

In this section, we give the successive steps of a proof of the persistence in a model of the form

$$(7)\qquad \left\{\begin{array}{lcl} \frac{ds}{dt} & = & \frac{1}{\varepsilon_1\varepsilon_2}\left(f(s)-g_1(s)x_1-g_2(s)x_2-g_3(s)x_3\right) \\ \frac{dx_1}{dt} & = & \frac{1}{\varepsilon_1}(g_1(s)-d_1)x_1 \\ \frac{dx_2}{dt} & = & (g_2(s)-d_2)x_2 \\ \frac{dx_3}{dt} & = & (g_3(s)-d_3)x_3 \end{array}\right.$$

where the occurring functions are differentiable, at least piecewise, ε_1 and ε_2 are **infinitesimal**[1]. The function f vanishes at 0 ; it is increasing then decreasing and vanishes at a value m. The functions g_i are zero at 0, increasing and bounded.

3.1. Oscillations of s and x_1. Let us consider the system

$$(8)\qquad \left\{\begin{array}{lcl} \frac{ds}{dt} & = & \frac{1}{\varepsilon_1}(f(s)-g_1(s)x_1) \\ \frac{dx_1}{dt} & = & (g_1(s)-d_1)x_1 \end{array}\right.$$

- Suppose that the nullcline $ds/dt=0$ is a curve φ that, when s increases from 0, decreases from $+\infty$ to a minimum value reached for $s=s^-$ then increases to a maximum value for $s=s^+$ to finally decrease and vanishes for $s=m$.
- Suppose that the value s^* such that $g_1(s^*)=d_1$ is between s^- and s^+.

Proposition 3.1. *For ε_1 **infinitesimal**, the system (8) has a limit cycle **close** to the curve $ABCD$ in Fig. 6.*

3.2. The Pontryagin-Rodygin's Theorem. Due to the lack of space, we shall try in these sections to avoid excessive mathematical formalism of the results and we refer to [12, 14, 13] for more details. To simplify, we suppose that all the occurring differential equations have the property of uniqueness of solutions. Let us consider the *slow and fast system*

$$(9)\qquad \left\{\begin{array}{lcl} \begin{bmatrix} \frac{ds}{dt} \\ \frac{dx_1}{dt} \end{bmatrix} & = & \frac{1}{\varepsilon}\begin{bmatrix} F(s,x_1,x) \\ G(s,x_1,x) \end{bmatrix} \\ \frac{dx}{dt} & = & H(s,x_1,x) \end{array}\right.$$

where the scalars s and x_1 are the *fast components*, and the vector x the *slow* one. The real number ε is positive and **infinitesimal**. The functions F, G and H are continuous. The following system, where x is considered as a parameter, is called the *fast equation*

$$(10)\qquad \begin{bmatrix} \frac{ds}{dt} \\ \frac{dx_1}{dt} \end{bmatrix} = \frac{1}{\varepsilon}\begin{bmatrix} F(s,x_1,x) \\ G(s,x_1,x) \end{bmatrix}$$

Hence, the (s,x_1)-component of a solution of (9) varies very quickly according to (10) where x has been frozen at its initial value. When the fast equation (10) has stable limit cycles Γ_x for each x in a compact domain, Pontryagin-Rodygin's

[1] We use N.S.A. terminology. Following the spirit of ([5]) when a word (like "infinitesimal") is written in bold character its meaning is the one used in the formal language of Nelson I.S.T. but the reader not familiar with this framework can use the intuitive meaning.

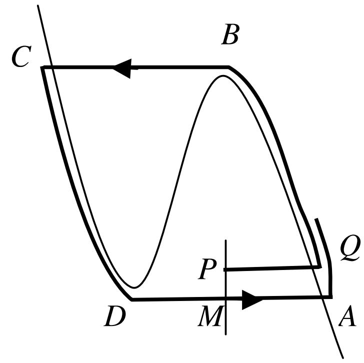

FIGURE 6. Starting from the point P the solution is **quasi horizontal** and goes **fast** to the nullcline $ds/dt = 0$; then the solution stays **near** the nullcline and goes up until it reaches the maximum at B; then the solution is **quasi horizontal** and goes **fast** to the nullcline $ds/dt = 0$ at point C ; then the solution stays **near** the nullcline and goes down until it reaches the minimum at D ; then the solution goes **fast** to the right to the nullcline $ds/dt = 0$ and reaches it at A.

Theorem [8] gives the limiting behavior of the singularly perturbed problem (9) : *Under suitable conditions, after a fast transition near the cycles described by the fast equation (10), the trajectories of (9) quickly roll up around the manifold generated by the cycles, with a slow evolution of the x-component according to the averaged system*

$$\frac{dx}{dt} = \frac{1}{P(x)} \int_0^{P(x)} H(s^*(\tau, x), x_1^*(\tau, x), x)\, d\tau \tag{11}$$

where $(s^*(\tau, x), x_1^*(\tau, x))$ is a $P(x)-$periodic solution of the fast equation corresponding to the cycle Γ_x. This result was originally obtained for at least C^2 vector fields, under the assumption that the cycles Γ_x are asymptotically stable in the linear approximation. However, the result obtained in [12] shows that Pontryagin-Rodygin description of solutions holds for C^0 vector fields under additional assumptions.

3.3. **Extension of Pontryagin-Rodygin's Theorem.** Note that System (7) has the form

$$\left\{ \begin{array}{rcl} \begin{bmatrix} \frac{ds}{dt} \\ \frac{dx_1}{dt} \end{bmatrix} & = & \frac{1}{\varepsilon_2} \begin{bmatrix} \frac{1}{\varepsilon_1} F(s, x_1, x) \\ G(s, x_1, x) \end{bmatrix} \\ \frac{dx}{dt} & = & H(s, x_1, x) \end{array} \right. \tag{12}$$

where $x = (x_2, x_3) \in \mathbb{R}^2$. The fast equation

$$\begin{bmatrix} \frac{ds}{dt} \\ \frac{dx_1}{dt} \end{bmatrix} = \frac{1}{\varepsilon_2} \begin{bmatrix} \frac{1}{\varepsilon_1} F(s, x_1, x) \\ G(s, x_1, x) \end{bmatrix} \tag{13}$$

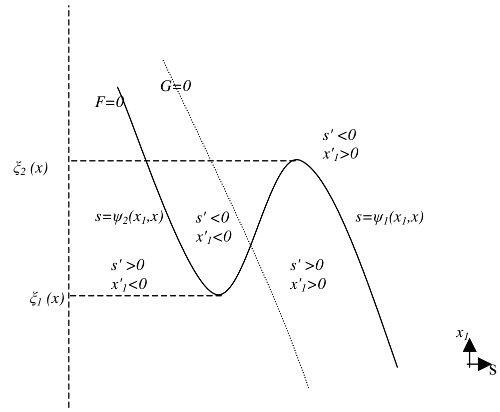

FIGURE 7. Notations in equations (14)

admits a stable limit cycle for any value of x for **infinitesimal** values of ε_1. It is tempting to apply Pontryagin-Rodygin's Theorem to (12) but the main reason that makes this impossible is the fact that the fast equation is a **nonstandard** equation. It is itself a singularly perturbed equation. We can not avoid to take into account the three dynamics of the problem. In [14] Pontryagin-Rodygin's Theorem is extended to this kind of system the fast equation of which admits a *slow and fast limit cycle*. This new result has also the advantage to overcome a serious limitation of Pontryagin-Rodygin's Theorem : unlike the latter, it makes possible the localization of the cycles, the approximation of their periods and the calculation of the average along these cycles. *The functions F, G and H being continuous and the positive real numbers ε_1 and ε_2 **infinitesimal**, suppose that there exists a compact domain K of $\mathbb{R}^2$ such that, for all $x \in K$ the nullclines $F = 0$ and $G = 0$ of (13) have the shape given in Figure 7. The (s, x_1)-plane is divided in four regions where the field has the indicated signs in the figure.* The limit cycle of (13) is **infinitesimally close** to the closed curve $(ABCD)$ in Fig. 6 formed by two "slow arcs" (AB) and (CD) and two "fast segments" (DA) and (BC). The two decreasing branches of the nullcline $F = 0$ are denoted $s = \psi_1(x_1, x)$ and $s = \psi_2(x_1, x)$. Let us define in the interior of K the *slow equation*

$$\frac{dx}{dt} = M(x), \tag{14}$$

where

$$\begin{aligned} M(x) &= \tfrac{1}{P(x)} \sum_{i=1}^{2} \int_{\xi_i(x)}^{\xi_{i+1}(x)} \tfrac{g(\psi_i(x_1,x),x_1,x)}{f_2(\psi_i(x_1,x),x_1,x)} dx_1, \\ P(x) &= \sum_{i=1}^{2} \int_{\xi_i(x)}^{\xi_{i+1}(x)} \tfrac{dx_1}{f_2(\psi_i(x_1,x),x_1,x)}, \text{with } \xi_3(x) = \xi_1(x). \end{aligned} \tag{15}$$

Let $\gamma(t)$ be the trajectory of a solution of (12). Theorem 5.2.1 page 75 in [14]

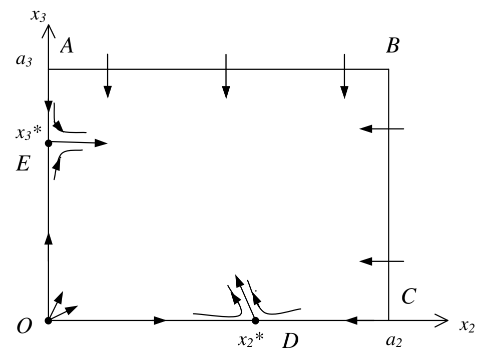

FIGURE 8. Portrait of (x_2, x_3) obtained from the averaged system (16). Compare to the simulations presented on Fig.5

explains how $\gamma(t)$ behave in the same manner than in the classical Pontryagin-Rodygin theorem, the averaging on the cycles being now well approximated by the explicit formulas (15).

3.4. **Application to the model.** Reconsider System (7).

- Assume that the functions g_2 and g_3 are zero until the respective thresholds s_2 and s_3 are reached such that $\min(s_2, s_3) \geq s^+$ and that g_2 and g_3 are increasing beyond.

This assumption allows us to assert that the subsystem

$$\left[\begin{array}{c} \frac{ds}{dt} \\ \frac{dx_1}{dt} \end{array}\right] = \frac{1}{\varepsilon_2}\left[\begin{array}{l} \frac{1}{\varepsilon_1}(f(s) - g_1(s)x_1 - g_2(s)x_2 - g_3(s)x_3) \\ (g_1(s) - d_1)x_1 \end{array}\right]$$

still admits, for every (x_2, x_3) and ε_1 small enough, a limit cycle Γ_{x_2,x_3} that differs from that of (8) for values of $s \geq \min(s_2, s_3)$. The more x_1 and x_2 are large, the more these cycles are distorted inwards in their right side. The minimum and maximum of the cycles remain unchanged. Here, the averaged equation (14,15) takes the form (see [14] for explicit formulas)

$$\left\{\begin{array}{l} dx_2/dt = x_2 M_2(x_2, x_3)/P(x_2, x_3), \\ dx_3/dt = x_3 M_3(x_2, x_3)/P(x_2, x_3). \end{array}\right. \tag{16}$$

A detailed study of equation (16) leads to the following conditions of persistence :

Theorem 3.2. [14] *Suppose that $s_3 > s_2 = s^+$, $\varphi(s_3) > \varphi(s^-)$ and that d_2 is below a certain constant well determined by the problem. Then, for $s_3 - s_2$ and d_3 small enough, there is persistence of the species x_2 and x_3 of (16).*

This result is reflected in Fig. 8 representing a positively invariant box $OABC$ of (16) in which arrive all trajectories with positive initial conditions. The axes are invariant, the origin O is an unstable node and C and E are saddle points. A lemma due to Butler-McGehee [2] shows that the union of limit sets of positive half-trajectories is a compact subset Ω which does not meet the axes.

Theorem 3.3. *Under the assumptions of the preceding Theorem, there is persistence of the whole species of the model (7) for all positive initial conditions.*

This final result is obtained by using a nonstandard permanence lemma [10] which extends the approximation of the component $(x_2(t), x_3(t))$ of the solution of (7) by the solution of (16) to an **infinitely large** time interval $[0, \omega]$. We than prove[2] that $(x_2(t), x_3(t))$ remains **infinitely close to** Ω for all **infinitely large** values of t and all **infinitesimal** values of ε_1 and ε_2.

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[2]We say that the **standard** set $\{\Gamma_{x_2,x_3} \times \{(x_2, x_3)\} : (x_2, x_3) \in \Omega\}$ is *practically asymptotically stable* for (7) for all **infinitesimal** values of ε_1 and ε_2 (see [13] for more details).